



Nat-Man WP7 report

prepared by members of Work-package7 in the Nat-Man project (Nature-based Management of beech in Europe) funded by the European Community 5th framework programme

Christensen, M.; Vesterdal, L.

Publication date:
2003

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Christensen, M., & Vesterdal, L. (2003). *Nat-Man WP7 report: prepared by members of Work-package7 in the Nat-Man project (Nature-based Management of beech in Europe) funded by the European Community 5th framework programme*. Nat-Man Working Report No. Vol. 25



NAT-MAN

Working Report 24

Physical and Chemical Properties of Decaying Beech Wood in two Danish Forest Reserves

Morten Christensen & Lars Vesterdal



*Deliverable 9 & 15 of the Nat-Man Project
Produced under Work-Package 7
2003*



The report is produced by the Nat-Man Project (Nature-based Management of Beech in Europe) co-ordinated by *Forest & Landscape Denmark*, and funded by the European Community 5th Framework Programme.
Contact: Co-ordinator Jens Emborg, jee@kvl.dk - The report is available at www.flec.kvl.dk/natman

NAT-MAN WP7 REPORT: DENMARK

Physical and chemical properties of decaying beech wood in two Danish forest reserves

Project leader:
Morten Christensen

Scientific contributors to WP7 (CWD characteristics and nutrients):
Lars Vesterdal, Morten Christensen, Jaris Bigler and Jacob Heilmann-Clausen

Christensen, M. & Vesterdal, L. 2003. Physical and chemical properties of decaying beech wood in two Danish forest reserves. Nat-Man Working Report 25.

ABSTRACT

The coarse woody debris (CWD) of beech was studied with respect to physical and chemical properties in two Danish forest reserves of long continuity, Suserup and Strødam. The amount of CWD in the two forests amounted to 41 and 36 Mg ha⁻¹, respectively. It was estimated that it takes about 50 years for logs to develop from decay class 1 to 5. There were clear differences in both physical and chemical properties of CWD assigned to five different classes of decay, and the patterns were quite similar between the two forests. The basic density of the wood decreased and the water content increased. The concentrations of nutrients either increased or were unchanged; N, P and S concentrations increased while concentrations of C and K showed no clear development from decay class 1 to 5. pH values, C/N ratios and C/P ratios all decreased from decay class 1 through 5. These changes may in part be attributed to the ability of decomposer organisms to retain some elements in the substrate while releasing others (e.g. C). The main difference between forests was that nitrogen concentrations of CWD tended to be slightly higher at Strødam than at Suserup.

Apart from being physical habitats for biodiversity, the CWD in the two forest reserves serves as important stores of carbon, nutrients and water for plants, fungi, microorganisms and animals. The C content of CWD would add about 80% to C content of the fine fraction of the forest floor and 15% to the C content of the whole soil to 1 m depth.

Introduction

Dead wood (coarse woody debris, CWD) is an important part of a natural forest ecosystem. In most managed forests in Denmark CWD is practically missing, and larger amounts of CWD are only found in forest reserves and other protected areas where forest management is less intensive. CWD has often been pointed out as one of the most important key habitats for forest biodiversity (Samuelsson 1994, Christensen and Emborg 1996). The role of CWD as storage medium for nutrients and water has also been emphasised (Harmon et al., 1986; Keenan et al., 1993), but there appears to be some controversy regarding its role for sustained forest productivity (Fahey, 1983; Harmon, 1986). More recently, carbon storage in biomass and soils has also been included among the valued functions of forests. In natural forests, CWD contributes to the pool of organic matter and thereby also to the ecosystem store of carbon. This store of carbon is not found in traditionally managed forests where exploitation of wood leaves only smaller branches to decay in the forest. In the effort to refine nature-based forestry and make more specific guidelines on how to handle CWD, there is a need for more knowledge of the amount of CWD and its physical and chemical properties along the continuum of decay in unmanaged Danish forests. The amount and properties of CWD in unmanaged forests may serve as a valuable reference for evaluation of silvicultural systems with respect to habitat for biodiversity and storage of carbon and nutrients.

The objectives of the study of beech CWD was to i) describe the physical and chemical properties at different stages of decay and ii) to quantify the carbon and nutrient storage in CWD of beech in unmanaged forests. The study was carried out in two Danish semi-natural forests, Strødam and Suserup.

Materials and methods

Sites

Two forest sites were selected for the study, Suserup Forest Reserve and Strødam Forest Reserve both located on Zealand in the eastern part of Denmark.

Suserup Forest Reserve

The reserve is an unmanaged mixed deciduous forest. Beech is the most dominating tree species constituting approx. 50 percent of the total basal area (Emborg et al., 2000). The standing (living) volume is estimated to 674 m³ per ha. The forest has been proposed to be close to a steady state equilibrium with an overall forest cycle of 284 years (Emborg et al., 2000).

Table 1. Site properties for Suserup Forest Reserve.

Study area	19.2 ha	Annual average temperature	8.1 C
Longitude	11 34' E	Coldest month (January)	0.8 C
Latitude	55 22' N	Warmest month (July)	16.7 C
Altitude	10-30 m	Average annual precipitation	644 mm

Strødam Forest Reserve

The reserve covers a total of 100 ha of forest of which 25.5 ha are unmanaged beech-dominated mixed deciduous stands with long history of non-intervention. Beech is highly dominant, only a few ash, oak, elm and birch occur in these areas. Standing (living) volume is estimated to 490 m³ per ha.

Table 2. Site properties for Strødam Forest Reserve.

Study area	25.5 ha	Annual average temperature	7.7 C
Longitude	12 16' E	Coldest month	-0.5 C
Latitude	55 58' N	Warmest month (July)	16.2 C
Altitude	15-25 m	Average annual precipitation	697 mm

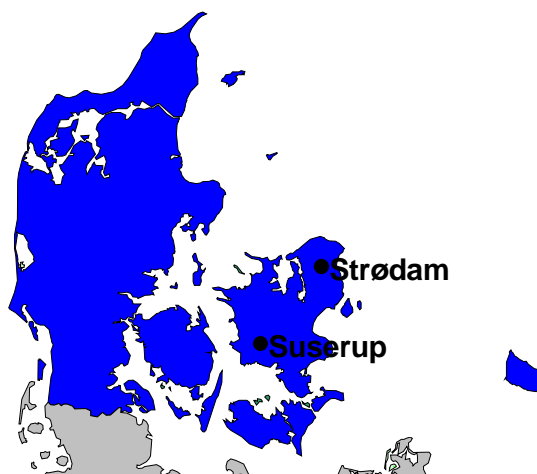


Figure 1. The locations of Suserup and Strødam forest reserves.

Sampling of wood

Selection of the CWD was carried out according to the agreed protocol (van Hees et al., 2003), however, CWD in decay class 6 was not sampled for density and nutrient analyses due to the pronounced contamination with mineral soil. Sampling was done in September 2000. The number of sampled logs is given in Table 3. Logs were all >20 cm dbh and included the bole of the tree. Wood samples for analysis were taken from outer surfaces towards the centre of the logs using drilling equipment. For all lying logs 6 samples were taken from different angles, except for the down-facing part. From snags higher than 2 meter, 6 samples were drilled from 6 different directions and in different heights ranging from 0.5 meter to 1.5 meter above the ground. All samples were ground and samples from each log and snag were pooled into a composite sample.

The forest reserves had previously been inventoried with respect to the volume of CWD. Large branches (>10 cm) were included in volume estimates.

Table 3. The number of sampled logs for nutrient analyses distributed to decay classes 1-5. There were no logs sampled for decay class 6.

	1	2	3	4	5	All decay classes
Suserup	1	3	6	5	7	22
Strødam	4	4	7	4	6	25
Total	5	7	13	9	13	47

To estimate wood density one piece of representative wood (approx. 3 x 3 x 3 cm) was taken from each log and snag. The collection was done during a rather moist winter (February 2002), suggesting that the wood moisture measured is close to the maximum "natural" level.

Age determination

Age of the dead log is defined as the time since death of the tree. The determination is made using three different methods listed according to prioritised rank below.

1. Data from ground floor registration. In Strødam a record of windthrown logs is available from 1980 and for a few logs even from 1967 (unpublished data). In Suserup all dead trees have been recorded since 1991 (J. Heilmann-Clausen & M. Christensen unpublished data)
2. A series of aerial photos with high resolution. The photos are taken with intervals of about three years and give an accuracy of +/- 2-4 year. The aerial photo method is only used in Suserup.
3. Small and medium sized trees close to the former position of the fallen or dead tree are selected to determine the time since growth was released. One core is taken from each tree using a 5 mm increment core. The tree rings are measured using a microscope and ADDO Årsringmätmaskin from Sweden

Decay classification (1-6)

Decay classes were defined according to the characteristics given in Table 4.

Table 4. Characteristics of the decay classes applied in Denmark.

Decay classes	Bark	Twigs and branches	Softness	Surface	Shape
1	Intact or missing only in small patches, more than 50%	present	hard or knife penetrate 1-2 mm	covered by bark, outline intact	Circle
2	Missing or less than 50%	only branches (>3 cm) present	hard or knife penetrate less than 1 cm	smooth, outline intact	Circle
3	Missing	missing	begin to be soft, knife penetrate 1-5 cm	smooth or crevices present, outline intact	Circle
4	Missing	missing	soft, knife penetrate more than 5 cm	large crevices, small pieces missing, outline intact	Circle or elliptic
5	Missing	missing	soft, knife penetrate more than 5 cm	large pieces missing, outline partly deformed	flat elliptic
6	Missing	missing	soft, partly reduced to mould, only core of wood	outline hard to define	flat elliptic covered by soil

Laboratory analyses of CWD

Nutrient and pH analyses:

All subsamples were dried at 40° C, ground (FRITSCH) and stored. A combined sample was formed for nutrient analyses from the stored subsamples (for logs and for snags separately).

Moisture

In the field 10-15 g of fresh wood sample was stored into weighing vessel of known mass. In the laboratory samples were weighed, then dried over night at 105°C and again weighed. Moisture content was calculated from sample weight loss.

Preparation of composite samples

For pH and nutrient analysis all subsamples were dried at 40° C and ground to particle size ~ 1mm. For each piece of CWD 10 ml of wood powder by subsample were blended into the composite sample. Only composite samples were analyzed for pH and nutrients.

pH analysis

A suspension of ground composite sample (2 g) and 20 ml purified water was prepared for pH determination. The suspension was shaken for 5 min. After 15 min pH was measured with combined glass pH electrode (TORELLI / ČUFAR 1995).

C, N and S analysis

The carbon, nitrogen and sulfur concentrations were determined with the element analyzer LECO CNS-2000. Wood composite samples (100-200 mg) were oxidized to carbon dioxide (CO₂), nitrogen oxides (NO_x) and molecular nitrogen (N₂) and sulfur dioxide (SO₂) at 1350°C. The amount of CO₂ and SO₂ was measured using an infrared detection method. After transforming of all nitrogen forms into N₂ by passing the combustion gasses over a Cu-catalysator, the content of N₂ was measured using thermal conductivity detection (<http://www.icp-forests.org/pdf/manual4.pdf>).

P and K analysis

For determination of P and K, composite samples were first digested in microwave oven (Milestone, Ethos) with HNO₃/HClO₄ 5:1 mixture. Phosphorus (P) was determined spectrophotometrically using ammoniumheptamolybdate as colour reagent. Potassium (K) was measured by AAS (Thermo Jarrel Ash, Scan 1). (<http://www.icp-forests.org/pdf/manual4.pdf>).

Basic wood density:

One piece of representative wood (approx. 3 x 3 x 3 cm) was taken from each log and snag. Moisture content was determined for the same pieces of wood immediately after sampling. Volumes were measured on wet samples (after at least 2 hour in water) in water and the dry weights were measured after drying at 105 C for at least 24 hours until the weight was stable.

Quality control

For all parameters, in each batch of samples one measurement of plant sample ALVA Probe 2/1999 was carried out to control quality of analysis.

Results and discussion

Quantity of dead wood

The amounts of living and dead wood and the amount of dead wood relative to living woody biomass is given in Table 5. Table 6 gives the distribution of dead wood to decay classes in absolute and relative terms.

Table 5: Amount of living woody biomass and dead wood and percent dead wood relative to living biomass in Strødam and Suserup forest reserve measured September 2000.

	Forest area (ha)	Living wood (m ³ /ha)	Dead wood (m ³ /ha)	Dead wood (%)
Suserup	19.2	674	168	24.9
Strødam	25.5	490	143	29.2

Table 6. The distribution of CWD volume (m³/ha) to decay classes 1-6.

	1	2	3	4	5	6	All decay classes
Suserup (m³/ha)	33.6	16.8	37.0	58.8	18.5	1.6	168
(%)	20	10	22	35	11	1	100
Strødam (m³/ha)	27.2	18.6	45.8	31.5	15.7	5.7	143
(%)	19	13	32	22	11	4	100

Decay class and age of dead wood

The data on the relation between age and degree of decay shows a rather large variation. Where 1st and 2nd decay class show a span of only a few years, decay class 3-5 show variation of more than 15 years (Fig. 2). These differences reflect a difference in the length of each class. It is important to be

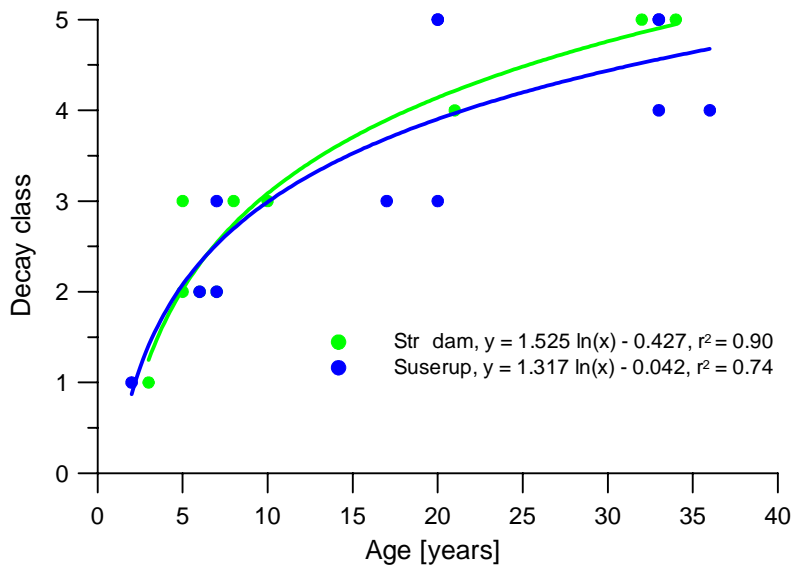


Figure 2. Relationship between decay classes and estimated age of CWD.

aware, that all classes are defined only by visible characteristics of the log surface, branches and shapes (Table 4). The total time for logs to reach decay class 5 is estimated to approximately 50 years dependent on the log size, the microclimatic variables and the composition of primary decomposers (Fig. 2). The patterns are similar for both sites.

Physical properties - moisture and basic wood density

The water content of logs showed a tendency to increase during the process of decay (Fig. 3). However, variation was large within decay classes, so decay class 1 and 5 did not clearly differ in water content. Water contents of individual log samples ranged from about 20% to 700% of the dry weight. The high moisture contents suggest that CWD can serve as an important storage medium for moisture in drier periods.

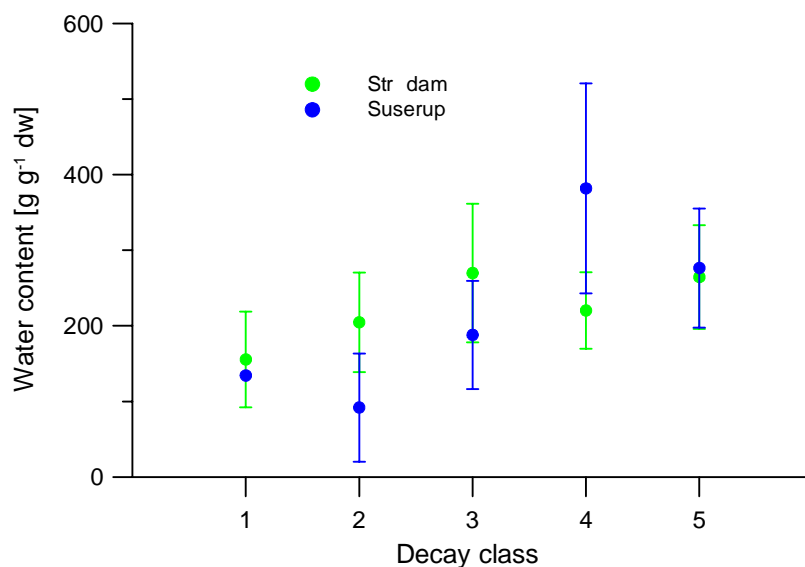


Figure 3. Water content of logs in the five decay classes. Bars indicate SEM except for decay class 1 at Suserup (n=1).

There was a clear pattern of decreasing wood density with increasing decay class at both sites (Fig. 4). The basic density of living beech wood (dry weight per fresh volume) is for Danish conditions estimated at 0.58 g cm^{-3} (Moltesen, 1988). The mean density of the logs in decay class 1 had already decreased to a mean of 0.34 for both sites, but the variability was high (range 0.16-0.52, n=5). In decay class 5, the mean for both sites was 0.17 (range 0.09-0.29, n=13). The loss of density reflects that logs do not just decompose from the surface and inwards. The most decomposable constituents within the wood is lost first due to the activity of fungi and wood boring insects which leaves the structural parts of the wood relatively intact. The basic density of CWD relative to living wood has therefore been used as an indirect measure of decay in order to quantify rates of decomposition for CWD (Christensen, 1984; Swift et al., 1976).

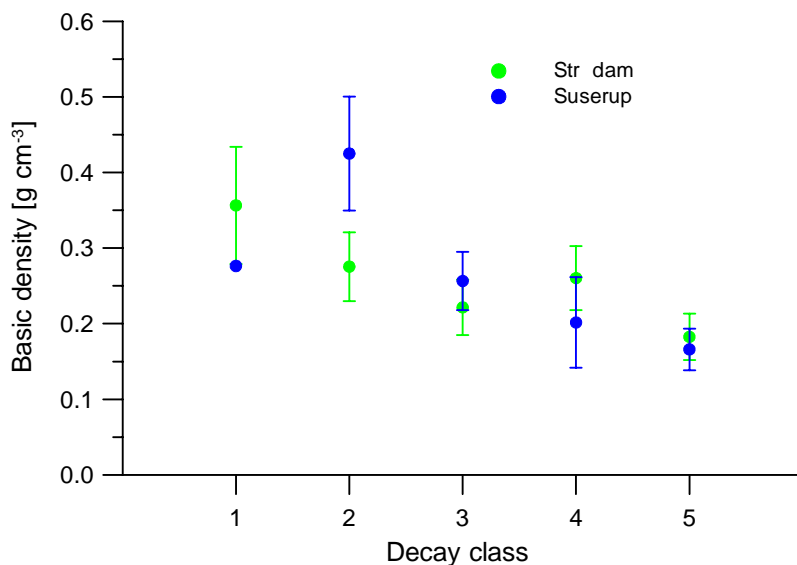


Figure 4. Decay class and basic wood density (dry weight per fresh volume). Bars indicate SEM except for decay class 1 at Suserup (n=1).

Carbon concentration

The carbon concentration was relatively constant along the continuum of decay with a mean value of 47% C (Fig. 5). A tight range of carbon concentrations close to 50% in decaying CWD was also reported from studies in the Harvard Forest (Currie and Nadelhoffer, 2002), Pacific Northwest (Keenan et al., 1993), Rocky Mountains (Laiho and Prescott, 1999) and from north-western Russia (Krankina et al., 1999). This is an indication that C is lost at approximately the same rate as mass during decay, which is also shown by the lack of relationship between wood density and C concentration (Fig. 6). Carbon stores in coarse woody debris may therefore be estimated from mass using a C concentration close to 50% regardless of decay class.

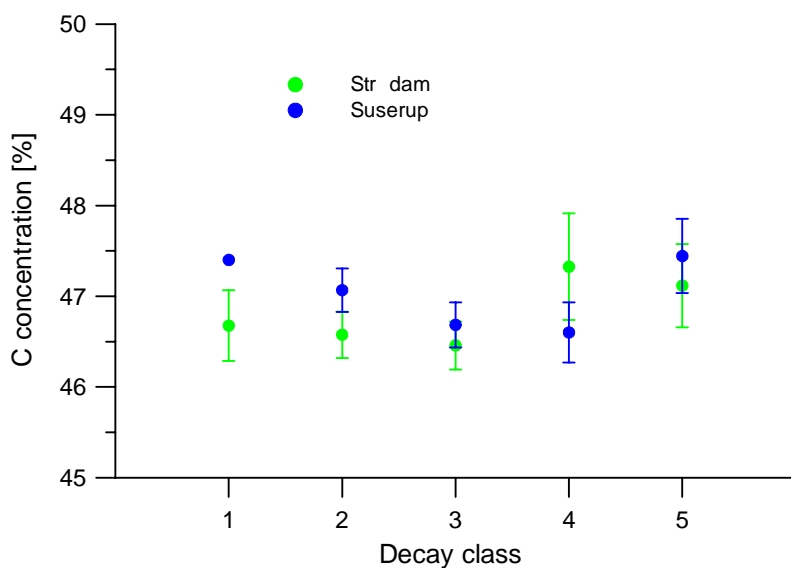


Figure 5. Carbon concentration of logs in the five decay classes. Bars indicate SEM except for decay class 1 at Suserup (n=1).

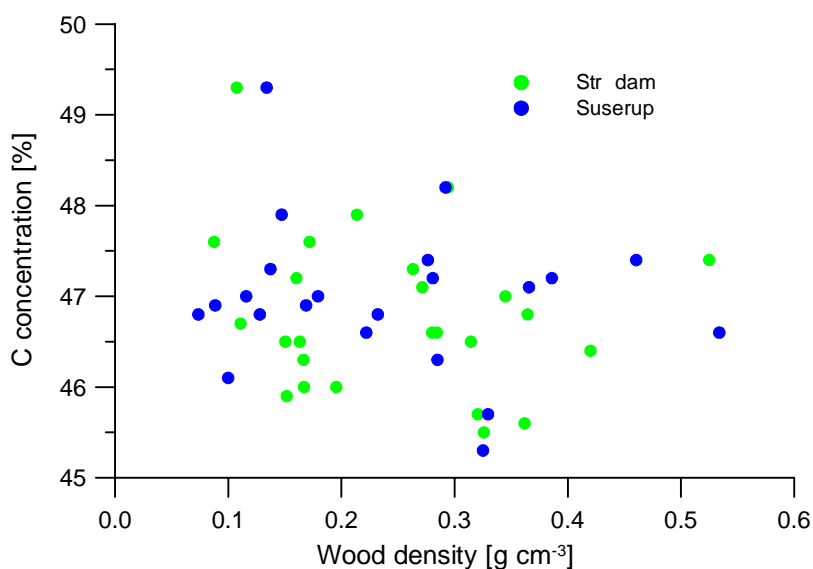


Figure 6. Wood density and carbon concentration

Nutrient concentrations and pH in wood of different decay classes

Nutrient concentrations are generally low in wood of living trees compared to other fractions of the biomass, e.g. bark, twigs, and especially foliage (Ponette et al., 2001). The nutrients included in this study (N, P, K and S) were also found in low concentrations in decay class 1. The pattern of nutrient concentrations along the decay continuum was quite similar for N, P and S in showing an increase with increasing decay class (Figs. 7a-c). On the other hand, K concentrations were not clearly related to decay class (Fig. 7d) and varied more or less within the same range for all decay classes.

The increases in N, P and S concentrations result from microbial immobilization of nutrients as the decay process proceeds. It is a well-known pattern from other studies of nutrient concentrations in different decay classes of CWD (Harmon et al., 1986; Krankina et al., 1999; Idol et al., 2001). While C is lost at the same rate as mass, other elements may be retained in the organic material or even transferred from the surrounding environment to increase the absolute content of the element. An enrichment with N and P may occur by canopy throughfall and also by transportation through fungal hyphae from more nutrient rich microsites in the surroundings (Staaf and Berg, 1982; Harmon et al., 1986). Nitrogen concentrations may also increase due to asymbiotic fixation of N by microbes (Brunner and Kimmins, 2003). This is also evident from the change in C/N and C/P ratios (Fig. 8), indicating that carbon is lost relative to N and P. It is a general picture that nutrients necessary for the metabolism of microbial organisms are retained in the biomass of microbes or in the substrate to improve the nutritional conditions and thereby facilitate digestion of the various carbon compounds. For log segments decomposing in Rocky Mountain forests, Laiho and Prescott (1999) found that there had been no net release of P after 14 years, and N had only been released from logs of tree species with relatively high initial N concentration in the wood.

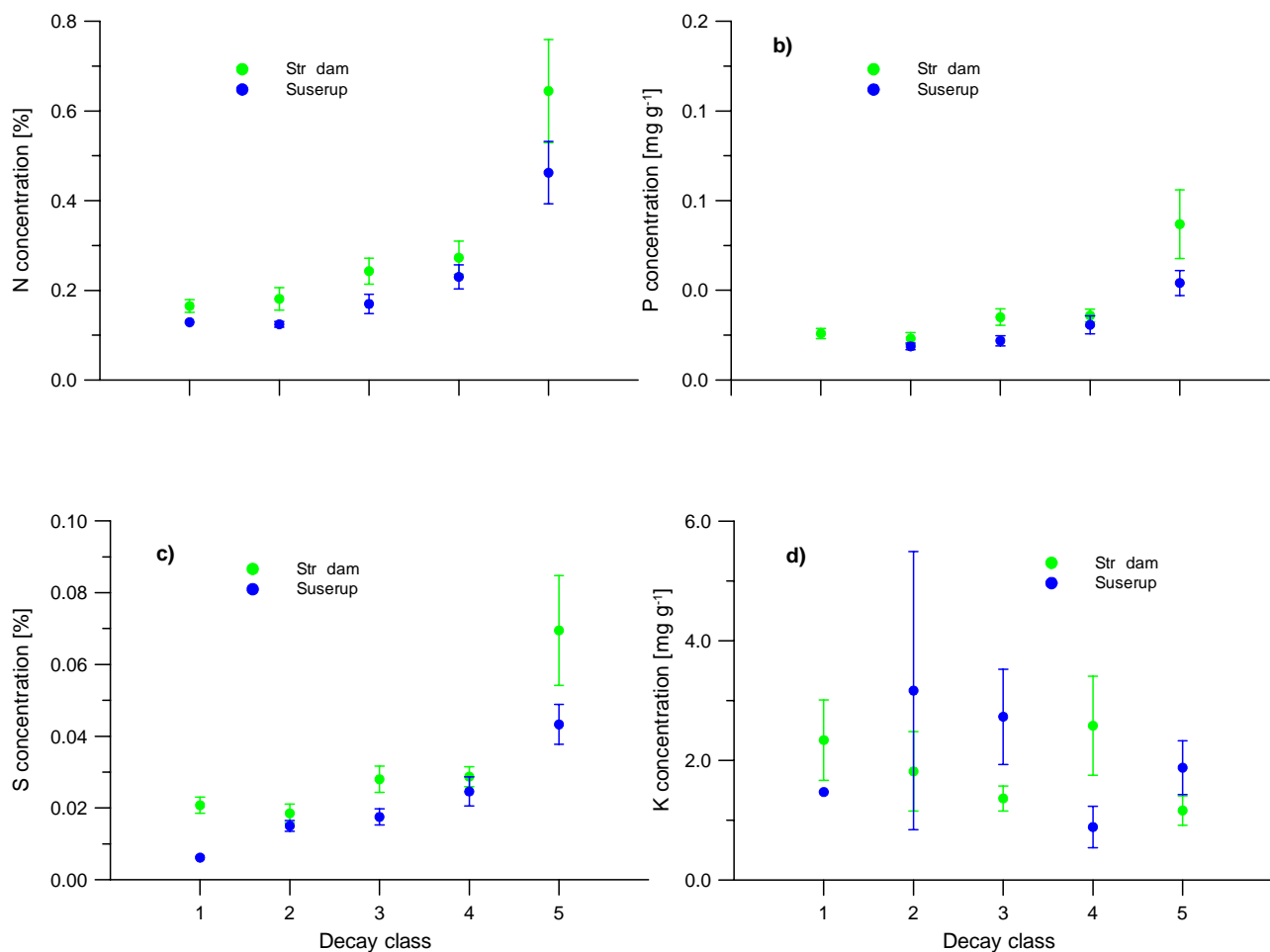


Figure 7. Concentrations of N (a), P (b), S (c), and K (d) in logs of different decay classes. Bars indicate SEM except for decay class 1 at Suserup (n=1).

The C/N ratios and to some extent also N concentrations were the only properties that seemed to differ between the two sites. CWD at Strødam had consistently higher N concentrations and consequently lower C/N ratios than CWD at Suserup for all decay classes. There was a tendency for the CWD at Strødam to also have slightly higher P and S concentrations than at Suserup, but this was less consistent for all decay classes. It is difficult to point at specific reasons for these site differences. The soil nutrient content is lower at Strødam than at Suserup, so the difference is probably not due to differences in initial nutrient concentrations of the wood. However, the difference in N concentrations and C/N ratios could be attributed to differences in N deposition between sites or to a difference between the decomposer communities at the two sites in their need to or capacity to immobilize N.

As opposed to N, P and S, K is known to be a much more mobile nutrient that is easily lost from decaying plant material by leaching. In a review, Harmon et al. (1986) concluded that leaching of K may also be significant from CWD during decay, although this has not been measured directly. In this study, there was no evidence of beech wood being depleted in K from decay class 1 to 5 (Fig.

7d). Krankina et al. (1999) also found little change in potassium concentrations of cwd of birch, spruce and pine over different decay classes.

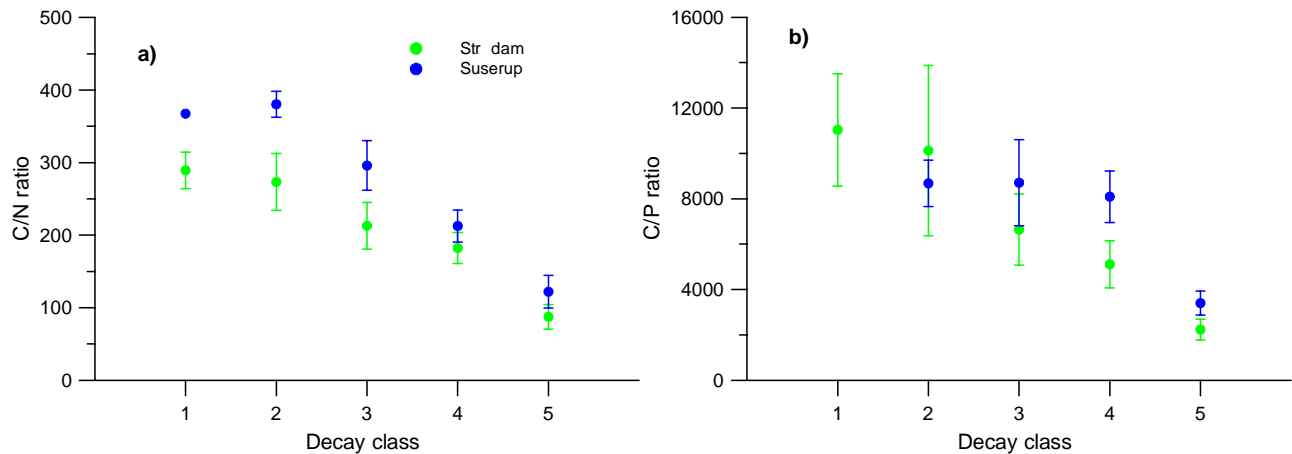


Figure 8. C/N ratios (a) and C/P ratios (b) in the five decay classes. Bars indicate SEM except for decay class 1 at Suserup (n=1).

There was also a clear change in pH of the decaying wood (Fig. 9), decreasing from about 5.5 to 4.5 from decay class 1 to 5. The decline in pH may be attributed to the organic acids originating from the decomposition process.

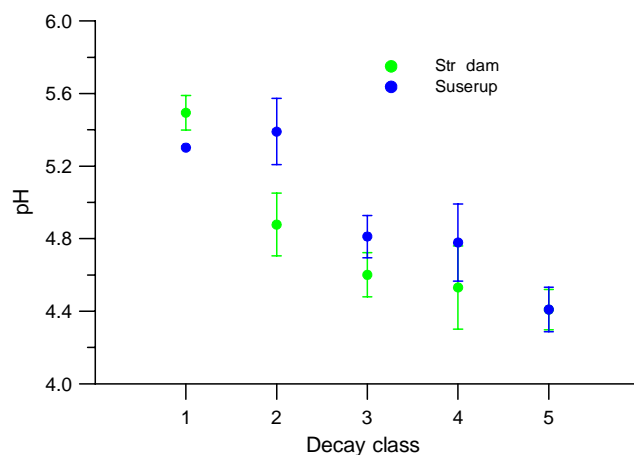


Figure 9. pH in the five decay classes. Bars indicate SEM except for decay class 1 at Suserup (n=1).

Biomass and the element and water contents of dead wood

The measured concentrations and wood densities within each decay class were combined with the estimated volumes of CWD to obtain the amounts of biomass, carbon and nutrient contents in CWD in the two forests (Table 7). As mentioned previously, CWD in decay class 6 was not sampled for density and nutrient analyses due to the pronounced contamination with mineral soil. The estimated

nutrient stores therefore only represents decay classes 1 to 5, which made up 96-99% of the CWD volume in the two forests (Table 6).

The CWD biomass was quite similar in the two forests. Slightly higher biomass, C content, K content and water content were found in Suserup which may be attributed to the higher volume of CWD. On the other hand, stores of N, P and S were highest at Strødam due to somewhat higher concentrations in CWD of these nutrients.

Table 7. Biomass, element and water contents of CWD in decay classes 1-5 in Suserup and Strødam.

	Suserup	Strødam
Biomass (Mg ha ⁻¹)	41.2	36.1
C (Mg ha ⁻¹)	19.3	16.9
N (kg ha ⁻¹)	78.8	90.4
P (kg ha ⁻¹)	2.9	3.4
S (kg ha ⁻¹)	8.3	10.2
K (kg ha ⁻¹)	85.8	70.5
Water (Mg ha ⁻¹)	91	79

The biomass of CWD in the two forests are well in line with amounts of CWD in mature and semi-natural deciduous forests summarized in the review by Harmon et al. (1986). Snag and log biomass for 200-year-old forests with a component of *Fagus* in North America were within the range of 30-50 Mg ha⁻¹ with lower amounts in younger forest stands. Idol et al. (2001) reported 59 Mg ha⁻¹ of CWD in a 150-year-old oak-hickory forest that had been subject to few selective thinnings.

As the two forests have been almost unmanaged the last 100 years, it is possible to estimate the natural amount of carbon that may be stored in CWD. This store of C is lost in traditionally managed forests, and it is relevant to quantify the significance of C stored in CWD for the total C storage of the ecosystem. Carbon may be sequestered in CWD over time after establishment of reserves of unmanaged forest or after a change in management to favour habitat for increased biodiversity. The amounts of C stored in CWD at Suserup and Strødam added 81% and 77%, respectively, to forest floor C pools that exclude CWD, i.e. the carbon stored in dead leaf and twig biomass on top of the mineral soil (Vesterdal et al., 2003). Currie and Nadelhoffer (2002) found that CWD in a 150-year-old *Quercus-Acer* forest added 48% C to the forest floor. Carbon in CWD at Suserup and Strødam amounted to about 15% of the total soil C store (Vesterdal et al., 2003).

The amounts of nutrients stored in CWD corresponds to 50-100% of the N and P stored in the fine fractions of the forest floor at comparable nutrient rich sites, e.g. about 100 kg N ha⁻¹ and about 6 kg P ha⁻¹ (Vesterdal and Raulund-Rasmussen, 1998). However, the K content of CWD was 8-10 times higher than that of the fine fraction of forest floors. The high K content may to some extent be caused by contamination of wood samples with soil particles.

Conclusion

The amount of CWD in the two forests amounted to 41 and 36 Mg ha⁻¹. It was estimated that it takes about 50 years for logs to develop from decay class 1 to 5. There were clear differences in both physical and chemical properties of CWD assigned to five different classes of decay, and the patterns were quite similar between the two forests. The basic density of the wood decreased and the water content increased. The concentrations of nutrients either increased or were unchanged; N,

P and S concentrations increased while concentrations of C and K showed no clear development from decay class 1 to 5. pH values, C/N ratios and C/P ratios all decreased from decay class 1 through 5. These changes may in part be attributed to the ability of decomposer organisms to retain some elements in the substrate while releasing others (e.g. C). The main difference between forests was that nitrogen concentrations of CWD tended to be slightly higher at Strødam than at Suserup.

Apart from being physical habitats for biodiversity, the CWD in the two forest reserves serves as important stores of carbon, nutrients and water for plants, fungi, microorganisms and animals. The C content of CWD would add about 80% to C content of the fine fraction of the forest floor and 15% to the C content of the whole soil to 1 m depth.

References

- Brunner, A., Kimmins, J.P., 2003. Nitrogen fixation in coarse woody debris of *Thuja plicata* and *Tsuga heterophylla* forests on northern Vancouver Island. Can. J. For. Res. (in press).
- Christensen, M., Emborg, J., 1996. Biodiversity in natural versus managed forest in Denmark. For. Ecol. Manage. 85, 47-51.
- Christensen, M., Hahn, K. (ed.) 2003: A study on dead wood in European beech forest reserves. Nat-Man Report.
- Christensen, O., 1984. The states of decay of woody litter determined by relative density. Oikos 42, 211-219.
- Currie, W.S., Nadelhoffer, K.J., 2002. The imprint of land-use history: patterns of carbon and nitrogen in downed woody debris at the Harvard Forest. Ecosystems 5, 446-460.
- Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. For. Ecol. Manage. 126, 173-189.
- Fahey, T.J., 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, Southeastern Wyoming. Ecol. Mon. 53: 51-72.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133-302.
- Idol, T.W., Figler, R.A., Pope, P.E., Ponder, F., 2001. Characterization of coarse woody debris across a 100 year chronosequence of upland oak-hickory forests. For. Ecol. Manage. 149, 153-161.
- Keenan, R.J., Prescott, C.E., Kimmins, J.P., 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island. Can. J. For. Res. 23, 1052-1059.
- Krankina, O.N., Harmon, M.E., Giazkin, A.V., 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can. J. For. Res. 29, 20-32.

Laiho, R., Prescott, C.E., 1999. The contribution of coarse woody debris to carbon, nitrogen and phosphorus cycles in three Rocky Mountain coniferous forests. *Can. J. For. Res.* 29, 1592-1603.

Moltesen, P. (1988). *Skovtræernes ved*. [The wood of forest trees]. Skovteknisk Institut, Akademiet for Tekniske Videnskaber. ISBN 87-87798-52-2.

Ponette, Q., Ranger, J., Ottorini, J.-M., Ulrich, E., 2001. Aboveground biomass and nutrient content of five Douglas-fir stands in France. *For. Ecol. Manage.* 141, 109-127.

Samuelsson, J., Gustafsson, L., Ingelög, T., 1994. Dying and dead trees - a review of their importance for biodiversity. Swedish Threatened Species Unit (Uppsala).

Staaf, H., Berg, B., 1982. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. *Can. J. Bot.* 60, 1561-1568.

Swift, M.J., Healey, I.N., Hibberd, J.K., Sykes, J.M., Bampoe, V., Nesbitt, M.E., 1976. The decomposition of branch-wood in the canopy and floor of a mixed deciduous woodland. *Oecologia* 26, 139-149.

Torelli, N., Čufar, K., 1995. Mexican tropical hardwoods. pH-value. *Holz als Roh- und Werkstoff* (Springer Verlag) 53, 133-134.

van Hees et al. 2003. Protocol on sampling of wood in NAT-MAN. In prep.

Vesterdal, L., Raulund-Rasmussen, K., 1998. Forest floor chemistry under seven tree species along a soil fertility gradient. *Can. J. For. Res.* 28, 1636-1647.

Vesterdal, L., Jørgensen, F.V., Callesen, I., Raulund-Rasmussen, K. (2003). Paired analysis of carbon storage in well-drained arable and forest soils in Denmark. (manuscript in prep.).